



## **Carbon Use Efficiency: Universal approach to link microbial growth, death, turnover and maintenance in steady state ecosystems**

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Carbon use efficiency (CUE) is a fundamental parameter of carbon (C) utilization by (micro)organisms and is central for understanding C and energy cycling. Originating from pure culture chemostat studies and based on biomass increase, the common CUE has many limitations for application in natural ecosystems (soils, aquatic systems, sediments), functioning under steady state and where microbial growth is compensated by death. To overcome the limitations of biomass based CUE, we suggest a CUE concept based on C utilization but independent on biomass changes, that can be applied for growing, constant, starving and dying microorganisms, as well as production of cellular and extracellular microbial compounds (storage or extracellular polysaccharides, exoenzymes). The suggested CUE is based on incorporation of the added C into microbial cells and its subsequent decrease with time because of maintenance (including cell internal recycling processes) and microbial turnover (growth and death). The CUE consists of 2 components: 1) maximal CUE calculated solely by biochemical pathways of organic compounds and 2) subsequent decrease of incorporated C amount during time because of two process groups: maintenance (cell internal metabolism) and turnover (microbial death and growth). The maximal CUE for most easily available monomers (glucose, pyruvate, amino acids) is close to 90%. This maximal CUE is a function of the substrate and pathway and is mainly independent on microbial group, physiological state, environmental conditions etc. To assess the second term – the decrease of CUE over time, we estimated the losses of C by microbial growth, death and maintenance – three topics central to understanding CUE in soil. Maintenance losses are by far not sufficient to explain the decrease of incorporated C as well as CO<sub>2</sub> fluxes from soil. Other process group is necessary – the microbial turnover, which includes growth and death – need at least 10 times higher C and energy costs. Microbial death is the result of predation by protozoa, nematoda, other animals and infection by phages. Death is compensated by microbial growth, for which the most energy of the incorporated substrate C (including cells of dead microorganisms) will be used. To maintain such C recycling, 1) the maximal CUE should be very high – 2-3 times higher than frequently estimated by traditional approach and 2) the portion of active microorganisms should be very low. The high CUE based on the fast microbial turnover is confirmed by various independent parameters of high microbial activity in soil, like high RNA/DNA, high ATP/ADP, <sup>13</sup>C incorporation into DNA, PLFA and other biomarkers, <sup>18</sup>O incorporation into DNA. These facts suggest continuous growth of microorganisms in soil, which is opposite to the common opinion that microorganisms in soil are solely under maintenance. The suggested CUE concept overcomes not only the previous limitations based on biomass increase, but also considers the time as main CUE factor; unifies CUE with maintenance and turnover, growth and death; works for individual cells and microbial communities; and reflects the stability of microbial life based on high efficiency of C recycling.